A FEW THINGS I WOULD LIKE TO KNOW ABOUT SOCIAL INSECTS

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Abstract: I describe eight open problems in the biology of social insects: 1) Can life cycles of individual organisms serve as a reliable model for the colony cycle? 2) Does the production of workers and sexuals in social hymenopterans fit the *bang-bang* model? 3) Do females in social hymenopterans have a smaller individual behavioural repertory than those of their solitary relatives? 4) Is memory in termite workers and soldiers limited to the sensory level? 5) Do some social wasps d/anor bees demonstrate coordinated colony defense? 6) Is there an induced defense in termite colonies at the level of caste proportions? 7) Are social wasps passing through a period of global population decrease? and 8) Is there a relationship between the level of primary production in the habitat and the proportion of social species among the insects?

Keywords: Bang-bang model, colony cycle, induced defense, social bee, social wasp, termites.

Introduction

Social insects are distinguished from the mass of solitary species by their habit of living in structured groups, or colonies. Although they comprise no more than 2% of insect species, they have attracted scientific and philosophical attention since ancient times. Almost all of them belong to four groups: a) termites (Blattaria: suborder Isoptera) with about 3000 species (Korb, 2021), b) social wasps (Hymenoptera: Vespidae) with about 1100 species (Jeanne, 2021), c) social bees with about 1000 species in various lineages of Hymenoptera (Engel et al., 2021), and d) ants (Hymenoptera: Formicidae) with about 12,000 described species (AntWeb, 2024).

The beginnings of insect sociobiology can be dated back about a century. Before that there were works on the biology of termites (Escherich, 1909; Hegh, 1922), social wasps (Réaumur, 1742), the western honey bee (Bevan, 1838; Butler, 1609; Huber, 1814; Purchas, 1657; Réaumur, 1740; Thorley, 1744), other social bees (Buttel-Reepen, 1903, 1915; Sladen, 1912), and ants (Emery, 1915; Escherich, 1906; Huber, 1810; Latreille, 1802; Wasmann, 1915; Wheeler, 1910). However, Wheeler (1923, 1928) was the first to treat the life of these insects generally. Several volumes of similar scope have appeared since then (Maidl, 1934; Wilson, 1971; Hermann, 1979-1982; Starr, 2021a).

During my senior year of high school, I got my own copy of Wilson's now classic (1971) *The Insect Societies*. I had just come to regard social insects as the most interesting aspect of the universe. Over the past 50 years I have posed a great many questions and hypotheses about these creatures. In some cases, I have managed to resolve one or another question (not necessarily by my own efforts). In others, I came to regard it as not so important. And there are others that remain unresolved and contribute to my bouts of insomnia. My purpose here is to describe eight of these questions that interest me, with some suggestions toward their resolution.

1. Can life cycles of individual organisms serve as a reliable model for the colony cycle?

Colonies of social insects have many features in common with individual animals. For over a century, it has been noted that colonies, like organisms, go through a cycle of foundation, growth, maturity, senescence, and death (Starr, 2021b). For this reason, they can be considered second-level organisms, or super-organisms (Hölldobler & Wilson, 2008; Starr, 2021c; Wheeler, 1911).

We have an impressive body of theory about the life cycles of individual plants and animals (Roff, 2002; Stearns, 1992, 2000). In contrast, colony cycle theory is much less mature, largely consisting of a series of analogies to life cycle theory. When reading works on life cycles, one could replace every mention of “life cycle” with “colony cycle” without it becoming absurd. Of course, what is not absurd and what is true are not necessarily the same. Do colony cycles follow patterns similar to life cycles? We do not know. There is hardly any body of theory on colony cycles as adaptive complexes. Rather than providing a body of conclusions, current concepts of life cycles provide us with a starting point for colony cycles.

There is no doubt that these analogies are a rich source of concepts and hypotheses (Bourke & Franks, 1995), but there is a risk of accepting them as already established. In the next period we must build a general theory of the colony cycle that will go beyond simple analogy to a more mature theory of the life cycle.

If there are significant differences between the two types of cycles, I predict that they will arise from the fact that the members of a colony, unlike the cells of the same body, are not a clone. That is, the members of the same colony do not have exactly the same interests regarding the production of new members.

A distinction is recognized between determinate and indeterminate cycles, analogous to the distinction between species whose individuals reproduce all their brood at once before dying (semelparity) and those that reproduce repeatedly (iteroparity) (Starr, 2021b). Among Neotropical social wasps, for example, all independent-founding species (*Mischocyttarus* and *Polistes*) are likely to have determinate colony cycles (Fig. 1a), whereas most swarm-founders (*Polybia* and related genera) have indeterminate cycles (Fig. 1c) (Starr, 2006). But we do not know this with certainty due to a paucity of basic data.

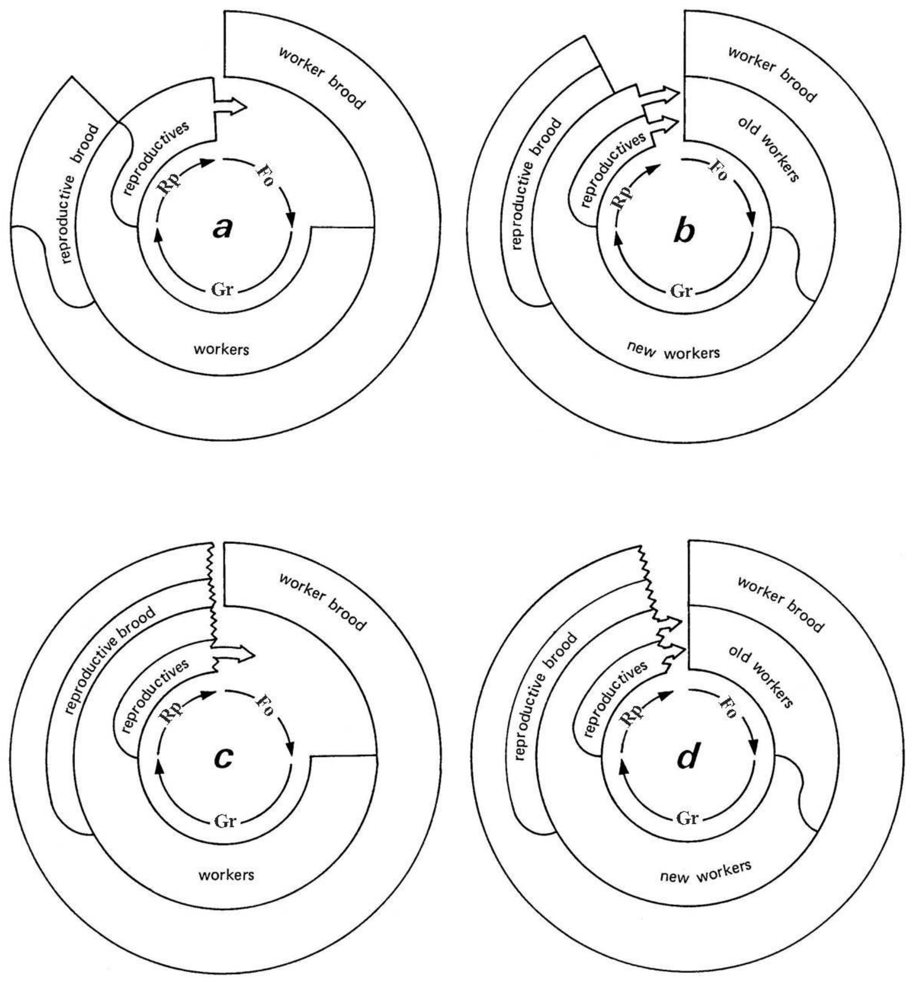

Fig. 1. The four basic types of the colony cycle in social insects. a. Independent foundation with a single phase of reproductive production. b. Swarm foundation with a single phase of reproductive production. c. Independent foundation with repeated phases of reproductive production. d. Swarm foundation with repeated phases of reproductive production. **Fo**, foundation phase. **Gr**, growth phase. **Rp**, reproductive phase. Modified from Starr (2006).

Tschinkel (1991) introduced the term *sociometry* for the analytical description of insect colonies. He emphasized that it was a neglected field of research, so that some important questions could hardly be made progress due to lack of basic data. Unfortunately, the collection of basic data is nowadays out of fashion.

As a first proposal towards such a conception in sociobiology, Tschinkel (1991: his Table 1) presented a list of 38 measurable aspects of the colony that he considered significant. Recognizing that the preparation of such a form, like the collection of data to fill it, must be a collective endeavor, he called for a discussion of this issue in the community of sociobiologists. To date, Tschinkel's (1991) work remains little discussed. At present, someone who needs a body of comparative data on some aspect of social insects usually searches the literature before making a call for unpublished data. For example, I have before me a message posted on an electronic network. The colleague is interested in comparing the longevity of queens from various groups; he has already extracted data on 62 species of ants and termites from the literature, and is asking for others.

This method of accumulating comparative data has been greatly facilitated by the Internet, but it is made unnecessarily difficult and slow by the lack of a public, searchable database on the model of the Human Relations Area Files, an anthropological database maintained at Yale University (https://hraf.yale.edu/). Given the existence of the International Union for the Study of Social Insects (IUSSI), it seems to me practicable to formulate a set of sociometric parameters as a collective project. I propose that the IUISI investigate the possibility of establishing and maintaining a permanent database on social insects.

2. Does the production of workers and sexuals in social hymenopterans fit the *bang-bang* model?

Colonies of social Hymenoptera produce reproductive individuals (queens and males) and non-reproductive individuals (workers). What is the temporal pattern of production of these two types of brood? At one extreme, the colony could produce both throughout the season (Fig. 2a), but this does not seem to occur in any species. Normally, a colony begins with the production of workers (foundation and growth phases), followed by brood destined to develop into queens and/or males laid (reproductive phase).

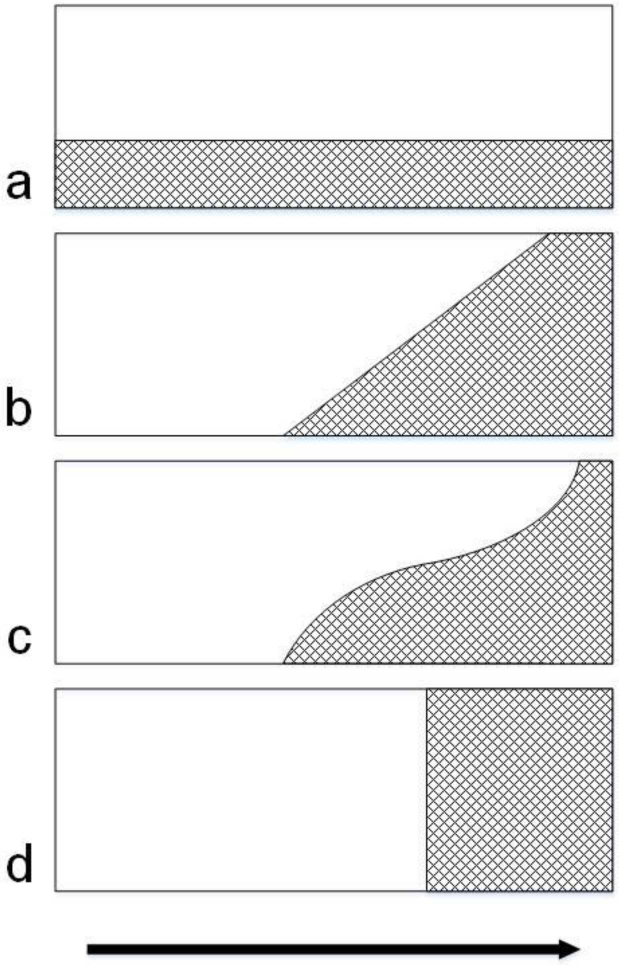

Fig. 2. Idealized patterns of worker brood (white) and reproductive (striped) egg production throughout the season (arrow). a. Regular throughout the cycle. b-c. Intermediate patterns, with partial overlap of the two phases. d. The two types of brood strictly separated (bang-bang). Figure by Nova Y. Starr.

3. **Do females of social Hymenoptera have a smaller behavioural repertory than those of their solitary relatives?**

According to the social brain hypothesis, the demands of social life in some vertebrate lineages have led to enlarged brains. It has been suggested that the same is true in Hymenoptera, that is, members of social species have larger brains relative to body size (Farris & Schulmeister 2010).

I suggest exactly the opposite. A female solitary wasp or bee has to do everything. She finds a nest site, builds and/or excavates the nest, lays eggs, forages, feeds larvae, and defends her brood against enemies. Females (queens and workers) of social Hymenoptera also undertake all of these tasks, but in a collective manner. In the case of highly social species, in particular, no individual does everything, even once in her life but is specialized. Morphological studies of the brain in various insects tend toward this hypothesis. In the social Hymenoptera investigated so far, the mushroom body (the part of the brain involved in memory and learning) is less developed in individuals with more specialized behaviour (O'Donnell 2021). This seems to imply that females of social species will be in some ways not as intelligent as solitary ones in the sense of having a more limited behavioural repertory. This hypothesis has its logic, but we have only just begun to know whether this perhaps the opposite better reflects reality. This question can be resolved directly by formulating ethograms of related social and solitary species. A complication arises when one considers that a large part of the activity occurs outside of the nest.

One can also ask whether solitary cockroaches have richer behavioural repertories than do eusocial cockroaches, i.e. termites. Many solitary cockroaches, as well as "lower" termites can be raised in the laboratory under almost natural conditions.

4. **Do termite workers and soldiers have a memory faculty that does not exceed the sensory level?**

Small animals necessarily have smaller and simpler brains (Eberhard & Wcislo 2012). However, some insects display impressive memory capacities. For example, a solitary wasp of the genus *Ammophila* maintains several active nests at once, remembering not only the location but also the state of each one (O'Neill 2001: Table 10-6). Some social insects are also notable for their memory powers. Foragers of the stingless bee *Melipona subnitida* Ducke can remember for 24 hours the daily period of best harvest of a given patch of flowers (Guimarães-Silva et al., 2021). A honey bee, having found a good source of nectar and/or pollen, can not only remember the location of the source for days, but also the colours of the flowers and even the approximate time of greatest productivity (Lindauer, 1971). And she can communicate its location to her nestmates by means of a dance, taking into account the movement of the sun (Couvillon, 2021). Likewise, the foragers of some ants show strong spatial orientation capacities, in at least one species even using patterns of the forest canopy (Hölldobler, 1980). In addition, a worker who moves away from her colony for a few hours does not forget its smell (Hölldobler & Wilson, 2008: 118).

These are examples of long-term memory, which acts for at least a few minutes. It is distinguished from short-term memory, which acts for less than a minute, and from ultra-short-term or sensory memory, which lasts less than a second. This latter is effectively a question of not forgetting what is perceived in the immediate moment.

The stigmergy theory in its original form (Grassé, 1959) is based on nest construction by "higher" termites. According to this, sometimes gigantic, complex, species-specific nests are formed by large numbers of tiny, generalized insects following an algorithm. An individual, encountering by chance any feature of the developing nest, responds in an innate, stereotypical manner appropriate to that feature. Differences between species in the rules of the algorithm can result in very different nests.

This model does not require a role for short-term memory, let alone long-term memory, just sensory memory. Furthermore, I am not aware of any worker or soldier activity -- with the possible exception of the few species that forage in the open -- that would seem to require a memory faculty of even one second. It occurs to me that termites might be the adult insects, whether solitary or social, that most of all lack a memory faculty.

This hypothesis has already been suggested in the popular press (Srinivasan, 2018): "Entomologists regard termites as unintelligent, as they lack memory and the ability to learn." Long-term memory, according to this view, is in some way a property of the colony, including its nest, and not of the individual. The hypothesis predicts a poorly developed mushroom body in the brain of non-reproductive termites (O'Donnell 2021).

5. Is there a coordinated response in defense of the colony in some social wasps and/or bees?

Approaching a colony of any *Polistes* species, you will observe that the wasps become alert (Fig. 3a). If you get closer still, they display a series of distinct and striking threats. And, if you continue to provoke them, they attack.

Fig. 3. Social wasps in alert state. Left: *Polistes crinitus* with exposed comb; all adults can see another animal approaching. Right: *Angiopolybia pallens* with combs inside an envelope; only some adults see outside the nest.

Often a multitude of wasps fly off at the same time, giving the impression of a coordinated attack. This suggests that a) the simultaneous attack is an illusion on our part, b) it is simply a matter of the same response threshold in many individuals, or c) there is visual communication between individuals, so that they fly simultaneously. This third possibility is the most interesting, since it implies a more sophisticated organization of defense, but we have no good evidence that this is really the case.

The same question arises in other social wasps and bees with covered nests, if many individuals look through the entrance or are on the surface (Fig. 3b). Although they do not have a visual threat system comparable to that of *Polistes*, they have the ability to fly together in attack. Similarly, collective defense of honey bees against an attack by the giant hornet *Vespa mandarinia* is well known (McClenaghan et al. 2019), but has not been shown to be coordinated. The resolution of this question will require a series of closely controlled observations in order to ensure a very regular provocation of the colony by raising the level.

6. **Is there an induced defense at the level of caste proportion in termites?**

When a self-defense trait develops because of previous attacks or threats, it is characterized as induced defense (Harvell, 1990). Some ants and most species of termites have a specialized caste for colony defense (soldiers). Since colonies of a given species and stage of development have a characteristic caste proportion, the question arises whether the colony produces a higher proportion of soldiers in response to repeated disturbances or threats.

To my knowledge, in the only experimental study of this question to date, colonies of the ant *Pheidole pallidula* (Nylander) increased the proportion of older workers (soldiers) when in the constant presence of a foreign colony of the same species. In control colonies, soldiers accounted for an average of 9.8% of workers, but almost twice as many in experimental colonies (Passera et al., 1996).

A resolution of this question regarding termites will be best done with a *Nasutitermes* species or another of the same subfamily, since they have a high proportion of soldiers (Fig. 4) (Haverty, 1977; Merritt & Starr, 2010).

Fig. 4. Workers and soldiers of *Nasutitermes* sp. Two workers on the right have a generalized body, while four soldiers on their left defend the colony with exposed glandular compounds from the proboscis. Photo by R.H. Scheffrahn.

Fig. 5. Nest of *Nasutitermes ephratae* with a triangular piece of the envelope removed.

Unlike ants, nasutitermitines and other termitids can hardly be kept in the laboratory except with their nest intact, which does not allow observations of what goes on inside. Such research would have to be done through field experiments. I suggest the following:

1. Identify a large number of active colonies of a single species in the same location.
2. Take a sample from each and calculate the soldier/worker ratio.
3. Divide the colonies at random into control and experimental groups.
4. At regular intervals over a few months disturb the experimental colonies by minimal destruction of their nests (Fig. 5), without affecting the control colonies.
5. Finally take new samples to compare the proportion of soldiers in the two groups.

7. **Are social wasps currently undergoing a general decline?**

There is a global crisis in populations of many amphibians. Herpetologists, like entomologists, have their field sites where they return year after year. In discussions at the First World Congress of Herpetology in 1989, many amphibian specialists learned that the perceived declines in their populations did not appear to represent isolated cases but a much broader pattern. In the following years it became established that there is in fact a deep and worldwide crisis in amphibian health due to multiple causes (Alford & Richards, 1999; Collins & Crump, 2009; Houlahan et al., 2000). More recently the specter of a similar pattern has been raised for insects. The great majority of long-term studies have been carried out in Europe and North America with an emphasis on butterflies (Dirzo et al. 2014; Wepprich et al. 2019). However, evidence is already emerging that this is a general and worldwide phenomenon (e.g., Hallmann et al., 2017, Sánchez-Bayo & Wyckhuys, 2019). It appears that different insect groups are not affected equally (Sánchez-Bayo & Wyckhuys, 2019). This raises the hitherto barely investigated question of whether social insects in general are affected differently from solitary insects due to living in relatively dense, cooperative groups. It is worth noting that the IUCN Red List of Threatened Species includes reports of almost 100 species of bumblebees (Hymenoptera: *Bombus*) and ants (Hymenoptera: Formicidae), and some halictid bees (Hymenoptera: Halictidae), but no social wasps (Baillie et al., 2004).

However, in recent years some social wasp specialists have come to suspect that a decline is underway in many populations (Table 1). For example, 15-20 years ago in my own area at the north-eastern corner of South America there were eight common species in the sense that I could have found at least one colony of any one per hour of searching. Today, only one of these species is still abundant, while the others are only found with difficulty. Furthermore, I am convinced by communications from several colleagues that the same thing is happening in other parts of the world for unknown reasons.

Populations of social wasps are perhaps more easily monitored than any other major group of social insects, as their nests are relatively conspicuous and species are relatively easily identified in the field. For this reason, we can have confidence in the preliminary data presented here. If a general decline in social wasps does result, what will be the most important causes? I doubt that global warming plays a key role. I also do not think it results from insecticide use, as a) these are applied mostly in agricultural habitats where there is a higher abundance of individuals, but low diversity, and b) in some places I have observed some abundant species despite heavy insecticide application. Furthermore, such application is not a recent phenomenon.

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Table 1. Examples of social wasps that were abundant in given localities 15-25 years ago, with their present status. **+** more common today. **0** no sustantial change. – distinctly less common today.

Pennsylvania, USA 41°N 79°W (R.S. Jacobson, pers. comm.)	
Dolichovespula arctica (Rohwer)	-
Dolichovespula arenaria (Fabr.)	-
Dolichovespula maculata (Linn.)	-
Polistes fuscatus (Fabr.)	0
Vespula acadica (Sladen)	-
Vespula alascensis Packard	-
Vespula consobrina (Saussure)	-
Vespula flavopilosa Jacobson	-
Vespula maculifrons (Buysson)	-
Vespula vidua (Saussure)	-
Ohio, USA 39°N 85°W (R.S. Jacobson, pers. comm.)	
Vespula maculifrons (Buysson)	-
Vespula squamosa (Drury)	-
Florida, USA 28°N 80°W (J.W. Wenzel, pers. comm.)	
Mischocyttarus cubicola Richards	_
Bangalore, India 13°N 78°E (R. Gadagkar, pers. comm.)	
Polistes stigma (Fabr.)	-
Ropalidia cyathiformis (Fabr.)	-
Ropalidia jacobsoni (Buysson)	-
Ropalidia rufoplagiata (Cameron)	-
Ropalidia variegata (Smith)	-
Trinidad, West Indies 11°N 61°W (C.K. Starr, pers. obs.)	
Metapolybia cingulata (Fabr.)	0
Mischocyttarus alfkeni (Ducke)	-
Mischocyttarus baconi Starr	-

Polistes lanio (Fabr.)	-
Polistes versicolor (Olivier)	-
Polybia occidentalis (Olivier)	-
Polybia rejecta (Fabr.)	-
Synoeca surinama (Linn.)	-
Monteverde, Costa Rica 10°N 85°W (S. O'Donnell, pers. comm.)	
Mischocyttarus mastigophorus Richards	-
Polybia aequatorialis Zavattari	0
Polybia raui Bequaert	0
Yaoundé, Cameroon 3°N 12°E (M. Tindo, pers. comm.)	
Belonogaster juncea (Fabr.)	-
Polybioides tabida (Fabr.)	-
Rio Claro, Brazil 22°N 48°W (E. Giannotti, pers. comm.)	
Polistes lanio (Fabr.)	-
Polistes simillimus Zikán	-
Protopolybia exigua (Saussure)	-
Protopolybia sedula (Saussure)	-
Asunción, Paraguay, 25°S 58°W (B.R. Garcete, pers. comm.)	
Mischocyttarus paraguayensis Bertoni	-
Polistes cavapyta Saussure	-
Polistes versicolor (Olivier)	-
Polybia ignobilis (Haliday)	-
Polybia occidentalis (Olivier)	-
Polybia sericea (Olivier)	-

8. **Is there a relationship between the level of primary production in the habitat and the proportion of social insects?**

The first attempt towards a general concept of the ecological impact of social insects in general was seen in the preparations for the International Biological Programme (IBP) of 1964–1974 under the leadership of M.V. Brian (1978). Already at that time, for example, the role of termites as agents of decomposition of plant matter, ants as important predators of terrestrial invertebrates, and bees as effective pollinators were recognized. Since then, progress has been slow towards a concrete answer to the questions “Do social insects as a whole have distinct roles in the environment?” and “What ecological difference arises from some lineages living in society?” The great success of social insects is easily seen in their high abundance/biomass and some of their impacts on the environment (e.g., Souza & Delabie, 2021). However, any relationship between their sociality and their ecological success is not obvious. In particular, what are the differences in their ecological effects between a colony of social insects and an equal number of related solitary insects?

Wilson (1987, 1990, 2012) and Hölldobler & Wilson (2008) propose an answer to this question: 1. Social insects dominate numerically in terrestrial habitats. 2. They also show dominance in harvesting the most valuable resources. 3. This dominance results precisely from their sociality. In this theory, highly social groups (termites, ants, and some bees) are at the top of the dominance pyramid. As a corollary, this dominance should appear more in the most stable and productive terrestrial ecosystems, especially in the tropics. This is a logical and very attractive thesis, and for this very reason it has been accepted too easily. That is, in its present form it suffers from an exaggeration of its empirical support.

Let us consider the first part. A well-known claim by Wilson (1990) is that “In the terra firme forest near Manaus, ants and termites together make up almost 30% of the animal biomass according to the results of Fittkau & Klinge (1973).” This figure of 30% of animal biomass has been repeated and popularized until many biologists accept it as a well-established figure for tropical forests in general (e.g., Bradley 2009). The reality is different. If one examines this claim in the works of several colleagues, it turns out that it is based on this single article from almost 50 years ago (Fittkau & Klinge 1973) with almost no replication or extension (e.g., Stork, 1987). Although quite plausible, we do not know for certain that social insects make up a greater proportion of individuals or biomass in tropical ecosystems than subtropical and temperate ones. Furthermore, the focus of this research was on vegetation, and animals were dealt with in a casual manner. Fittkau & Klinge (1973) openly stated that “The lack of exact data on the population density and biomass of termites and ants – so abundant in the central Amazonian environment – is regrettable. We can only refer to Beck’s (1971) conjecture that three-quarters of the soil fauna in the central Amazonian forest, in terms of biomass, are ants and termites. It is therefore impossible for us to assess the role of these soil animals in the energy flow in the central Amazonian forest.” Today we have an estimate of the global biomass of ants, with the unsurprising result that it is higher in tropical and subtropical regions (Schultheiss et al. 2022). What we do not know even approximately is how the biomass of social and solitary insects varies geographically.

This lack of knowledge is an opportunity for organized science. I suggest that entomological societies, including the Andean-Caribbean Section of the IUSSI, consider organizing collaborative research on this problem.

Acknowledgements

This essay is dedicated to the memory of Edward O. Wilson (1929-2021), a pioneer in the study of social insects. The first version of it was presented shortly before Wilson's 90th birthday at a meeting of the International Union for the Study of Social Insects (Andean-Caribbean Section), whose members I thank for their comments. The journal’s editor and reviewers also contributed valuable suggestions.

References

Alford, R.A., & Richards, S.J. (1999). Global amphibian declines: A problem in applied ecology. *Annual Review of Ecology and Systematics*, *30*, 133-165.

AntWeb. (2024). Version 8.112. California Academy of Science, https://www.antweb.org. Accessed 2 Oct. 2024.

Baillie, J., Hilton-Taylor, C., & Stuart, S.N. (2004). *2004 IUCN Red List of Threatened Species: A Global Species Assessment*. Cambridge: IUCN 191 pp.

Beck, L. (1971). Bodenzoologische Gliederung und Characterisierung des amazonischen Regenwaldes. *Amazoniana*, *3*, 69-132. (Cited from Fittkau & Klinge 1973).

Bevan, E. (1838). *The Honey Bee: Its Natural History, Physiology, and Management*. London: John van Voorst 447 pp.

Bourke, A.F.G., & Franks, N.R. (1995). *Social Evolution in Ants*. Princeton: Princeton Univ. Press 529 pp.

Bradley, T.J., Briscoe, A.D., Brady, S.C., Contreras, H.L., Danforth, B.N., Dudley, R., Grimaldi, D., Harrison, J.F., Kaiser, J.A., Merlin, C.N., Reppert, S.M., Vandenbrooks, J.M., & Yanoviak, S.P. (2009). Episodes in insect evolution. *Integrative & Comparative Biology*, *49*, 590-606.

Brian, M.V. (1978). *Production Ecology of Ants and Termites*. Cambridge: Cambridge Univ. Press 416 pp.

Butler, C. (1609). *The Feminine Monarchie*. Oxford: Joseph Barnes.

Buttel-Reepen, H. (1903). *Die stammesgeschichtliche Entstehung des Bienenstaates, sowie Beiträge zur Lebensweise der solitären und sozialen Bienen (Hummeln, Meliponen, etc.)*. Leipzig: G. Thieme 138 pp.

Buttel-Reepen, H. (1915). *Leben und Wesen der Bienen*. Braunschweig: Friedrich Vieweg 300 pp.

Collins, J.P., & Crump, M.L. (2009). *Extinction in Our Times: Global Amphibian Declines*. Oxford: Oxford Univ. Press 304 pp.

Couvillon, M.J. (2021). Communication: honey bee dances. Pp. 256-260 in: Starr, C.K. (ed.*)*. *Encyclopedia of Social Insects*. Cham, Switzerland: Springer.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., & Collen, B. (2014). Defaunation in the Antropocene. *Science*, *345*, 401-406.

Eberhard, W.G., & Wcislo, W.T. (2012). Plenty of room at the bottom? *American Scientist*, *100*, 226-233.

Emery, C. (1915). *La Vita delle Formiche*. Turin: Bocca 251 pp.

Engel, M.S., Rasmussen, C., & González, V.H. (2021). Bees: Phylogeny and classification. Pp. 93-109 in: C.K. Starr (ed.), *Encyclopedia of Social Insects*. Cham, Switzerland: Springer.

Escherich, K. (1906). *Die Ameise, Schilderung ihrer Lebensweise*. Braunschweig: Friedrich Vieweg 232 pp.

Escherich, K. (1909). *Die Termiten oder weißen Ameisen*. Leipzig: Werner Klinkhardt 198 pp.

Farris, S.M., & Schulmeister, S. (2010). Parasitoidism, not sociality, is associated with the evolution of elaborate mushroom bodies in the brains of hymenopteran insects. *Proceedings of the Royal Society Biological Sciences 278* (1707), 940-951.

Fittkau, E.J., & Klinge, H. (1973). On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica, 5,* 2-14.

Grassé, P.-P. (1959). La reconstruction du nid et les coordinations interindividuelles chez *Bellicositermes natalensis* et *Cubitermes* sp. La théorie de la stigmergie: Essai d'interprétation du comportement des termites constructeurs. *Insectes Sociaux 6*, 41-80.

Greene, A. (1984). Production schedules of vespine wasps: An empirical test of the bang-bang optimization model. *Journal of the Kansas Entomological Society, 57*, 545-568.

Guimarães-Silva, A., Carvalho, G.C.A., Miranda, A.C. de, Contrera, F.A.L., & Rêgo, M.M.C. (2021). Temporal memory in foraging of the stingless bee *Melipona subnitida* (Hymenoptera: Apidae: Meliponini). *Sociobiology, 68*(2), e5863.

Hallmann, C.A.; Sorg, M., Jongejans, E., Siepel, H., Holfland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & Koon, H. de. (2017). More than 75 per cent decline over 27 years in total insect biomass in protected areas. *PLoS ONE, 12*, e0185809.

Harvell, C.D. (1990). The ecology and evolution of inducible defenses. *Quarterly Review of Biology*, *65*, 323-340.

Haverty, M.I. (1977). The proportion of soldiers in termite colonies: A list and a bibliography (Isoptera). *Sociobiology*, *2*, 199-216.

Hegh, E. (1922). *Les Termites*. Vol. 1. *Partie Générale*. Brussels: Imprimerie Industrielle & Financière 756 pp.

Hermann, H.R. (1979-1982). *Social Insects*. Vol. 1-4. New York: Academic 437, 491, 416, 385 pp.

Hölldobler, B. (1980). Canopy orientation: A new kind of orientation in ants. *Science, 210,* 86-88.

Hölldobler, B., & Wilson, E.O. (2008). *The Superorganism*. New York: W.W. Norton 544 pp.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., & Kuzmin, S.L. (2000). Quantitative evidence for global amphibian population declines. *Nature*, *404*, 752-755.

Huber, F. (1814). *Nouvelles Observations sur les Abeilles*. 2nd ed. Vol. 1-2. Paris: J.J. Paschoud 362, 479 pp.

Huber, P. (1810). *Recherches sur les Moeurs des Fourmis Indigènes*. Paris: J.J. Paschoud 328 pp.

Jeanne, R.L. (2021). Swarm-founding wasps. Pp. 918-934 in: C.K. Starr (ed.), *Encyclopedia of Social Insects*. Cham, Switzerland: Springer.

Korb, J. (2021). Termites. Pp. 952-960 in: C.K. Starr (ed.), *Encyclopedia of Social Insects*. Cham, Switzerland: Springer.

Latreille, P.A. (1802). *Histoire Naturelle des Fourmis, et Receuil de Mémoires et d'Observations sur les Abeilles, les Araignées, les Faucheurs, et Autres Insectes*. Paris: Théophile Barrois 445 pp.

Lindauer, M. (1971*). Communication among Social Bees*. Cambridge: Harvard Univ. Press 161 pp.

Maidl, F. (1934). *Die Lebensgewohnheiten und Instinkte der staatenbildenden Insekten*. Vienna: Fritz Wagner 823 pp.

McClenaghan, B., Schlaf, M., Geddes, M., Mazza, J., Pitman, G., McCallum, K., Rawluk, S., Hand, K. & Otis, G.W. (2019). Behavioral responses of honey bees, *Apis cerana* and *Apis mellifera*, to *Vespa Mandarina* marking and alarm pheromones. *Journal of Apicultural Research*, *58*, 141- 148.

Merritt, N.R.C., & Starr, C.K. (2010). Comparative nesting habits and colony composition of three arboreal termites (Isoptera: Termitidae) in Trinidad & Tobago, West Indies. *Sociobiology*, *56*, 611-622.

O'Donnell, S. (2021). Brain development and brain evolution. Pp. 131-133 in: C.K. Starr (ed.), *Encyclopedia of Social Insects*. Cham, Switzerland: Springer.

O'Neill, K M. (2001). *Solitary Wasps*. Ithaca: Cornell Univ. Press 406 pp.

Oster, G.F., & Wilson, E.O. (1978). *Caste and Ecology in the Social Insects*. Princeton: Princeton Univ. Press 352 pp.

Passera, L., Roncin, E., Kaufmann, B., & Keller, L. (1996). Increased soldier production in ant colonies exposed to intraspecific competition. *Nature*, *379*, 630-631.

Purchas, S. (1657). *A Theatre of Politicall Flying-Insects*. London: Thomas Parkhurst 207 pp.

Réaumur, R.A.F. de. (1740). *Mémoires pour Servir à l'Histoire Naturelle des Insectes*. Vol. 5. Paris: Imprimerie Royale 728 pp.

Réaumur, R.A.F. de. (1742). *Mémoires pour Servir à l'Histoire Naturelle des Insectes*. Vol. 6. Paris: Imprimerie Royale 608 pp.

Roff, D.A. (2002). *Life History Evolution*. Sunderland, Massachusetts: Sunderland 527 pp.

Sánchez-Bayo, F., & Wyckhuys, K.A.G. (2019). Worldwide decline in the entomofauna: A review of its drivers. *Biological Conservation*, *232*, 8-27.

Schultheiss, P., Nooten, S.S., Wang, R., Wong, M.K., Brassard, F., & Guénard, B. (2022). The abundance, biomass, and distribution of ants on Earth. *Proceedings of the National Academy of Sciences*, *119*(40), p.e2201550119.

Sladen, F.W.L. (1912). *The Humble Bee -- its Life-History and How to Domesticate it*. London: Macmillan 283 pp.

Souza, H.J. de., & Delabie, J.H.C. (2021). Ecosystem engineers: ants and termites. Pp. 347-352 in: C.K. Starr, (ed.), *Encyclopedia of Social Insects*. Cham, Switzerland: Springer.

Srinivasan, A. (2018). Busy bodies. *New Yorker*, 17 Sept: 26-31.

Starr, C.K. (2006). Steps toward a general theory of the colony cycle in social insects. Pp. 1-20 in: V.E. Kipyatkov (ed.), *Life Cycles in Social Insects*. St Petersburg: St Petersburg Univ. Press.

Starr, C.K. (2021a). *Encyclopedia of Social Insects*. Cham, Switzerland: Springer 1049 pp.

Starr, C.K. (2021b). Colony cycle. Pp. 225-230 in: C.K. Starr (ed.), *Encyclopedia of Social Insects*. Springer. Cham, Switzerland.

Starr, C.K. (2021c). Superorganism concept. Pp. 913-918 in: C.K. Starr (ed.), *Encyclopedia of Social Insects*. Cham, Switzerland: Springer.

Stearns, S.C. (1992). *The Evolution of Life Histories*. London: Oxford Univ. Press 249 pp.

Stearns, S.C. (2000). Life history evolution: successes, limitations, and prospects. *Naturwissenschaften*, *87*, 476-486.

Stork, N.E. (1987). Guild structure of arthropods from Bornean rain forest trees. *Ecological Entomology*, *12*, 69-80.

Thorley, I. (1744). *Melissologia, or the Female Monarchy, Being an Enquiry into the Nature, Order and Government of Bees*. London: John Thorley 206 pp.

Tschinkel, W.R. (1991). Insect sociometry, a field in search of data. *Insectes Sociaux*, *38*, 77-82.

Wasmann, E. (1915). *Das Gesellschaftsleben der Ameisen*. Vol. 1. Münster: Aschendorff 413 pp.

Wepprich, T., Adrian, J.R., Ries, L., Wiedemann, J., & Haddad, N.M. (2019). Butterfly declines over 20 years of systematic monitoring in Ohio. *PLoS ONE*, *14*(7), e0216270.

Wheeler, W.M. (1910). *Ants: Their Structure, Development and Behavior*. New York: Columbia Univ. Press 663 pp.

Wheeler, W.M. (1911). The ant colony as an organism. *Journal of Morphology*, *22*, 307-325.

Wheeler, W.M. (1923). *Social Life among the Insects*. New York: Harcourt, Brace 375 pp.

Wheeler, W.M. (1928). *The Social Insects: their Origin and Evolution*. Londong: Kegan Paul, Trench, Trubner 378 pp.

Wilson, E.O. (1971). *The Insect Societies*. Cambridge: Harvard Univ. Press 548 pp.

Wilson, E.O. (1987). The causes of ecological success: the case of ants. *Journal of Animal Ecology*, *56*, 1-9.

Wilson, E.O. (1990). *Success and Dominance in Ecosystems: The Case of Social Insects*. Oldendorf/Luhe: Ecology Institute 104 pp.

Wilson, E.O. (2012): *The Social Conquest of Earth*. New York: W.W. Norton 330 pp.